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Swimming Tracks of *Aplysia brasiliana,* with Discussion of the Roles of Swimming in Sea Hares

by

P. V. HAMILTON

Department of Biology, University of West Florida, Pensacola, Florida 32514, U.S.A.

Abstract. Surface-swimming *Aplysia brasiliana* were tracked at two locations in southwest Florida in order to document the magnitude of movement that can be achieved by this method of locomotion. Twenty sea hares released near a shoreline swam for a median duration of 9.9 min and traveled a median distance of 52 m. One animal swam continuously for 114 min in a weak to slack current, and traveled 953 m. Sea hares released in a lagoon influenced by tidal currents showed a tendency to swim for shorter periods in stronger currents. The swimming tracks of some sea hares were influenced by physical features in their environment.

INTRODUCTION

ALTHOUGH MOST GASTROPOD mollusks are exclusively benthic and locomote only by crawling, some normally benthic species occasionally swim (FARMER, 1970). Twelve of the *Aplysia* species recognized by EALES (1960) have been observed swimming. Sea hares swim using two large flaps (the parapodia) which project dorsolaterally from the foot. The biomechanics of swimming and its neuromotor control are described by VON DER PORTEN *et al.* (1982) and previous workers.

Other research has examined the orientation of swimming and the modulation of water speed in *Aplysia brasiliana* (HAMILTON & AMBROSE, 1975; HAMILTON & RUSSELL, 1982a, b; HAMILTON, 1984). Because these studies involved analyses of only short periods (60 or 90 sec) of swimming, and because the popular neurophysiological model, *A. californica,* apparently does not swim at all, some biologists may assume that aplysiid swimming is an ecologically insignificant behavior. The literature contains few details on the duration of uninterrupted swims, and no information on tracks of uninterrupted swims or on the effect of current conditions on swimming. In order to document the role of swimming as a means of achieving significant horizontal movement in sea hares, I present here some simple descriptive data for the uninterrupted swimming tracks of 40 animals released at two locations exposed to different current conditions. Tracks were recorded for released animals, instead of for animals found swimming naturally, so that the time and location where swimming began could be known accurately.

MATERIALS AND METHODS

Sea hares, *Aplysia brasiliana* Rang, were studied in Charlotte County, Florida (for map see HAMILTON & RUSSELL, 1982a:fig. 1). Adult animals (200–970 g) were collected from shallow-water grassbeds or, within 3 h after sunrise, from beaches where they had become stranded by overnight high tides. They were maintained in floating cages up to 4 d before release, and were fed *Hypnea* and other red algae, their natural food (KRAKAUER, 1971).

The first set of releases was conducted at Mote Beach, on the northeast shore of Placida Harbor. Currents at Mote Beach are primarily influenced by wind-driven waves rather than tidal changes (HAMILTON & RUSSELL, 1982a). Tall trees grow supratidally, and a band (10–25 m wide) of sand bottom slopes gradually ($<3°$) from the high tide line to lower intertidal and subtidal grassbeds. During the releases water depth varied from 20 to 60 cm at the single release point within the band of sand bottom, and current speeds were slack to weak. Each animal was held on the bottom, facing offshore, for 10 sec before release.

The second set of releases was conducted in B3 Lagoon, which comprises one of several connections between Gasparilla Pass (which opens to the Gulf of Mexico) and Gasparilla Sound. The Lagoon is well protected from wind and waves, but strong tidal currents occur there. Each sea hare was removed from a floating cage anchored near the shore and transported quickly by boat to a release site. Animals were released at several sites near the center of the rectangular-shaped lagoon, depending on current con-

Table 1

Characteristics of uninterrupted swims by 20 sea hares released at Mote Beach during slack to weak current conditions.

Variable	Minimum	Maximum	Median
Swim duration (min)	4.5	114.0	9.9
Swim distance (m)	24	953	52
Ground speed (m/min)	2.5	9.2	5.3

ditions, but all sites were in water deeper than 5 m. Each sea hare was hand-placed into the water and gently agitated until it began to flap the parapodia and swim freely. Current speed beneath a bridge at one end of the Lagoon was classified as strong, moderate, weak, or slack for each release.

At both Mote Beach and B3 Lagoon, swimming sea hares were tracked by rowing 2–4 m behind them in a small boat. An animal had to swim for at least 3 min after release to be tracked, for reasons described in the Results. Directions were measured to the nearest 1° with an aimable prismatic compass. Directions to two or (usually) three landmarks were recorded from the point of release, along the swimming track at 3-min intervals thereafter, and from the point where an animal stopped swimming or was lost from sight. A map of each release area was made using a USGS map for Placida, Florida (N2645-W8215/7.5) and on-site measurements of distances and directions between landmarks. Data on directions to landmarks were used to plot positions along swimming tracks. Track lengths were measured using a curvimeter. For the Mote Beach tracks, a directness (or straightness) value was computed for each track as described in HAMILTON (1977). Median values and ranges are used to summarize durations and distances of swims because the frequency distributions of both variables were positively skewed.

RESULTS

About 60 sea hares were released at Mote Beach during slack to weak current conditions. A frequency distribution of the swim durations for these 60 animals would show two distinct groups or modes. About 40 sea hares swam for less than 1.5 min. Grassbeds located 5 to 6 m offshore from the release point were reached by all sea hares in about 1 min, and about 40 animals immediately dove to the bottom upon reaching these grassbeds. Twenty sea hares did not dive to the bottom upon reaching the grassbeds, and swam longer than 3 min; their mode was in the 9–10 min range.

The swimming tracks for the latter group of 20 sea hares are summarized in Table 1. These sea hares trav-

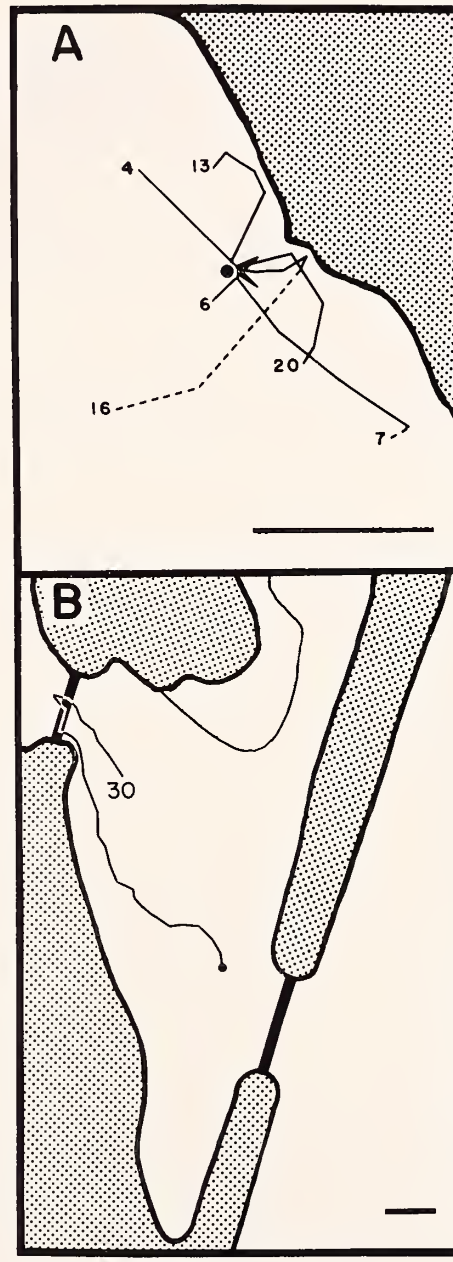

Figure 1

Sea hare swimming tracks may be influenced by physical features in their environment. A. Swimming tracks of the six sea hares that were released at Mote Beach and began swimming in the onshore direction. All six eventually reversed their heading, thus avoiding becoming stranded. Dashed lines for animals #7 and #16 indicate swimming tracks subsequent to brief stops on the bottom. B. Swimming track of one animal (#30), released in B3 Lagoon, that reversed its heading after passing beneath the bridge and swam back into the Lagoon against a weak outgoing tide. This type of response has been observed in other sea hares. Scale bars are 50 m.

Table 2

Characteristics of uninterrupted swims by 20 sea hares released at B3 Lagoon during two current conditions.

Variable	Minimum	Maximum	Median
Current moderate to strong (n = 9)			
Swim duration (min)	3.0	33.5	7.8
Swim distance (m)	88	673	237
Ground speed (m/min)	15.6	43.5	30.3
Current slack to weak (n = 11)			
Swim duration (min)	6.0	87.0	21.0
Swim distance (m)	24	469	120
Ground speed (m/min)	2.9	10.1	6.7

eled at a median ground speed of 5.3 m/min for a median duration of 9.9 min, and covered a median distance of 52 m. One animal swam for 114 min and traveled 953 m from the release point. The track directness (straightness) values for 14 of the 20 sea hares were greater than 0.9, thus revealing considerable ability to maintain a relatively straight track over time. Five of the six sea hares with values less than 0.9 started swimming in the onshore direction, and subsequently reversed their headings (see below and Figure 1A).

About 80 sea hares were released in B3 Lagoon. As for Mote Beach, a frequency distribution of the swim durations for these 80 animals would show two distinct modes. About 60 sea hares dove to the bottom and were lost from sight within about 10 sec after release. Twenty animals did not dive immediately, and swam longer than 3 min; their mode was in the 7–8 min range.

The range of current conditions occurring in B3 Lagoon permitted examination of the effect of current on swimming tracks at a single location. The 20 tracked sea hares were divided into two groups according to the current conditions during their release. Their swimming tracks are summarized in Table 2. Because swimming *Aplysia* cannot achieve water speeds greater than about 14 m/min (HAMILTON, 1984), the median ground speed of 30.1 m/min for sea hares released in moderate to strong currents clearly reflects the contribution of tidal current to horizontal displacement. Although it is not surprising that sea hares traveled at lower ground speeds and moved shorter distances when released in slack or weak currents, it is surprising that such sea hares swam for longer periods than those released in stronger currents. The swim durations for the moderate-strong group (median = 7.8 min) and slack-weak group (median = 21.0) are significantly different (Mann-Whitney $U = 77.5$; $P < 0.05$).

The tracks of two groups of sea hares seemed to be influenced by physical features in their environment. At Mote Beach, six of the 20 tracked sea hares began swimming in the onshore direction (Figure 1A), but all eventually reversed their heading and began swimming offshore. Animals #6, #13, #16, and #20 all entered water shallower than about 12 cm, but did not touch bottom, before reversing their headings. Animal #6 reversed its heading at about T = 2 min, and so it had already moved back offshore when its T = 3 min position was recorded. Animal #16 stopped swimming soon after heading offshore.

At B3 Lagoon, undisturbed sea hares swimming on an outgoing tide have often been observed passing beneath the bridge at one end of the Lagoon. Although such animals do not appear to have similar headings when they are still some distance from the bridge, many swing around and adopt an up-current heading as they get about 10–15 m from the bridge. Despite their swimming efforts, a strong tidal current carries them backward, beneath the bridge and out into Gasparilla Pass. Five of the 20 sea hares tracked in B3 Lagoon passed beneath bridges, and adoption of an up-current heading was observed in two of the five. The heading change was quite striking for animal #30, which was released on a weak outgoing tide, and which eventually swam back into the Lagoon from beneath the bridge (Figure 1B).

Thirty-eight of the 40 sea hares tracked at Mote Beach and B3 Lagoon dove to the bottom or were lost from sight in water 1–5 m deep. Most of these animals began making short "excursion" dives down to as much as 50–100 cm beneath the surface, a few minutes before their final dive or loss from sight. Although the rate of parapodial flapping was not recorded for any animal, sea hares seemed to swim normally during both the descending and ascending phases of excursion dives.

DISCUSSION

Sea hares released at both study sites formed two distinct and natural groups according to swimming time: those which swam only until they reached a nearby grassbed (less than 90 sec) or which immediately dove to the bottom, and those which swam longer than 3 min. The purpose of this study was to document how far and how long *Aplysia brasiliana* are capable of swimming. Consequently, this study focused on the behavior of the second group.

The data presented here should be considered minimum estimates of the swimming capabilities of the tracked sea hares. Wave height, sky conditions, water turbidity, and swimming depth all influenced how long an animal could be kept in view. All distances traveled by the tracked sea hares are underestimated because positions were recorded only once every 3 min, and the actual paths during these 3-min intervals were never perfectly straight.

The influence of current speed in B3 Lagoon on ground speed and swimming distance was expected, and is probably due to passive displacement effects of current on swimming animals. However, the significant influence of current speed on swimming duration must involve an active response by animals, and this suggests an ability to detect current speed. It would be interesting to learn how current speed is detected. Sea hares were released from a drifting boat, so they were essentially up-to-speed with the water mass from the time they commenced swimming. The Thrust Modulation Response (TMR) of *Aplysia brasiliana* involves detection of current direction, and it is influenced by current speed (HAMILTON, 1984).

The heading reversals of those sea hares that almost stranded on the shore at Mote Beach (Figure 1A), and the up-current headings adopted by some sea hares as they pass beneath bridges in B3 Lagoon (Figure 1B), may both depend on visual detection of objects above the water's surface (*e.g.,* bridge, treeline). HAMILTON & RUSSELL (1982b) demonstrated that, under field experimental conditions, an unblocked view of the sky is required for sea hares to maintain a consistent swimming direction. *Littorina irrorata,* a gastropod possessing eyes of a similar design yet half the size of those possessed by *Aplysia,* can detect bar-shaped targets filling as little as 1° of visual arc (HAMILTON & WINTER, 1982; HAMILTON *et al.,* 1983). Regardless of the mechanisms involved in the heading reversals of sea hares at Mote Beach, this response suggests that those few animals that oriented onshore during previous studies (HAMILTON & AMBROSE, 1975; HAMILTON & RUSSELL, 1982a) eventually would have turned around had they been allowed to swim for longer than 60 or 90 sec.

The adaptive function of swimming in *Aplysia* has not been studied systematically, but several hypotheses exist. In at least some other opisthobranchs (*e.g.,* EDMUNDS, 1968), swimming seems to serve as an escape response from benthic predators. However, the sea hare's swimming capabilities seem far too sophisticated for just this function, and no evidence supports this hypothesis exclusively. It is clear that sea hares that are stranded on gradually sloping beaches or sand bars can use swimming to move into deeper water, if they are resubmerged by a subsequent high tide before succumbing to desiccation and insolation stresses. Swimming probably enables sea hares to move within or between grassbeds on a daily basis. The adaptive value for such movements could involve searches for prospective mates, concentrations of algal food, or more suitable physicochemical conditions.

Finally, swimming may facilitate seasonal migration in *Aplysia brasiliana.* An incursion of sea hares into shallow water occurs in south Florida during the early spring (HAMILTON *et al.,* 1982), the period of peak algal abundance. By late summer, sea hares are not found in shallow water, where water temperatures approach or exceed the lethal limit (27–31°C). A similar seasonal pattern of *A. brasiliana* abundance in shallow water was reported for the southern hemisphere by SAWAYA & LEAHY (1971), who also suggested a migration hypothesis. Seasonal movements between deep and shallow water could be assisted by directionally advantageous tidal currents. Direct evidence of migration, in the form of movement records of tagged individuals, is lacking for all opisthobranchs and most other mollusks suggested to migrate (HAMILTON, 1985).

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